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On the Fructification of Neuropteris heterophylla, Brongniart

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PHILOSOPHICAL TRANSACTIONS.

I. *On the Fructification of* Neuropteris heterophylla, Brongniart.

By Robert Kidston, *F.R.S., L. and E., F.G.S.*

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[Plate 1.]

Evidence has been slowly gathering during the last few years that some carboniferous plants, which had previously been classed as Ferns, differ from true Ferns in many important points, and that perhaps a more correct definition of these fossils would be "fern-like plants." For this group Potonié has proposed the name of *Cycadofilices*.*

Until quite recently the group has depended entirely on characters derived from the anatomical structure of the stems of the plants which had been placed in it, as none of the numerous fructifications or seeds which occur in the rocks along with the stems of the *Cycadofilices*, could definitely be referred to any individual of the group.

Early in the present year, Professor Oliver and Dr. D. H. Scott communicated a paper to this Society, "On *Lagenostoma Lomaxi*, the seed of *Lyginodendron*";† and though the seeds there described were not organically united to *Lyginopteris* (*Lyginodendron*) *Oldhamia*, the structure of the glands on the cupule which surrounds the seed and the organisation of the bundle in the pedicel agree so entirely with the corresponding structures in *Lyginopteris Oldhamia*, that one can scarcely doubt the correctness of the conclusion arrived at by these botanists, that *Lagenostoma Lomaxi* is the seed of *Lyginopteris Oldhamia*. Their investigations have shown that "in the most general relations" of the organisation of *Lagenostoma Lomaxi* "the seed approaches the Gymnospermous type." There is, therefore, in *Lyginopteris Oldhamia*, which cannot be distinguished in its vegetative organs from *Sphenopteris Höninghausi*, Brongt.,‡ a type of plant combining Cycadean as well as Filicinean characters.

It seems, therefore, impossible to doubt any longer that many of our so-called carboniferous Ferns belong to the same transitionary type, and it has been shown by Renault§ and Grand'Eury,‖ that the petioles of some *Alethopteris*, *Neuropteris* and

* Potonié, 'Lehrb. d. Pflanzenpalæontologie,' p. 160, 1899.

† 'Roy. Soc. Proc.,' vol. 71, p. 477, 1903.

‡ Brongniart, 'Hist. d. Végét. Foss.,' vol. 1, p. 199, Plate 52.

§ Renault, "Étude du Genre *Myelopteris*," 'Mém. présentés par Divers Savants à l'Acad. d. Sciences de l'Institut de France,' vol. 22, No. 10, p. 21, 1876.

‖ Grand'Eury, 'Flore Carbon. du Départ. de la Loire et du Centre de la France,' p. 130, 1877.

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Sphenopteris have a *Myelopteris* structure, a structure which WEBER and STERZEL* have shown was possessed by the petioles of *Medullosa*, and which is further illustrated in the petioles of *Medullosa anglica*, SCOTT, whose stem exhibits the typical organisation of the *Cycadofilices*.†

The chief point which still remains to be determined is the nature and form of the pollen members of the various indivduals of the *Cycadofilices*, for the presence of a seed demands the presence of an antheroid member for its pollination. Dr. SCOTT seems to favour the view that these may be found in *Calymmatotheca*, and this view may ultimately be found to be correct, but there is at present no satisfactory evidence to support it. My own opinion is that in *Calymmatotheca* we are dealing with *Sporangia*. One point is certain, that in the Lower Coal Measures, where *Lyginopteris Oldhamia* (or *Sphenopteris Höninghausi*) occurs, *Calymmatotheca* must be very rare, as I have not met with a single specimen from that horizon, and in the Middle Coal Measures, where *Sphenopteris Höninghausi* is also found, I can only remember of having seen two specimens, both belonging to the *Calymmatotheca asteroides* LESQX. sp.‡

Neuropteris heterophylla, BRONGNIART.

Plate 1, figs. 1–9.

The late Dr. STUR was the first botanist to express any doubt as to *Neuropteris* being a true Fern,§ and this opinion he based on the fact that no fruiting specimen of *Neuropteris* had ever been discovered, and as many other fossil Ferns showed their fructification on the fronds, had *Neuropteris* possessed an ordinary form of Fern fructification, in such a common and widely distributed genus surely some trace of it would have been discovered. Of course there was the possibility of the barren and fertile fronds being quite dissimilar in appearance, a not uncommon occurrence amongst carboniferous Ferns.

A few years earlier, RENAULT published his Memoir on the genus *Myelopteris*, in which he adopted the opinion that the affinities of *Myelopteris*, some of which were referable to the *Neuropterideæ* (*Neuropteris* and *Odontopteris*), were with the *Marattiaceæ*.‖ This opinion was accepted generally as fixing the place of *Neuropteris*

* WEBER and STERZEL, "Beitr. z. Kenntnis d. *Medulloseæ*," 'Bericht. d. Naturwis. Gesell. zu Chemnitz,' vol. 13, p. 43 (84), 1896.

† SCOTT, "On *Medullosa anglica*, a New Representative of the Cycadofilices," 'Phil. Trans.,' B, vol. 191, pp. 81–126, 1899.

‡ See ZEITLER, "Observations sur quelques fougères des dépôts houillers d'Asie Mineure," 'Bull. Soc. Bot. de France,' vol. 44, p. 199, 1897; also 'Éléments de Paléobot.,' pp. 83 and 129.

§ STUR, "Morphologie und Systematik der Culm- und Carbonfarne," p. 6, 1883 ('Sitzb. der k. Akad. der Wissensch.,' I. Abth.).

‖ RENAULT, 'Étude du Genre *Myelopteris*,' *loc. cit.*, p. 21.

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among the true Ferns. It has, however, been already mentioned that *Myelopteris* has been found to be the petiole of *Medullosa*, a most characteristic member of the Cycadofilices, and this important discovery opens up the whole question of the affinities of *Neuropteris*, and has given rise to the opinion that it is also one of the large though not very well defined group of the *Cycadofilices*,* and this view of the affinities of *Neuropteris* is now confirmed by the discovery of fruiting specimens with the pinnules of *Neuropteris heterophylla*, BRONGT., still attached to the pedicel which bears the seed.

In 1887 I described a small fertile specimen of *Neuropteris heterophylla*, BRONGT., which was discovered by Mr. T. STOCK, in the Lower Coal Measures of Blairpoint, Dysart, Fife.† This specimen (Text figure 1) shows an axis about 8 centims. long, which gives off lateral pinnæ. Both the pinnæ and terminal portion of the axis end in slender naked dichotomously divided branchlets, terminated by an imperfectly preserved small body, which appears to be split into four arms or valves, but the structure of these terminal bodies cannot be clearly made out. This specimen, except in showing that this fertile portion was deprived of the ordinary foliage leaves (though these are borne below the fertile part and allowed of a satisfactory identification of the species), only indicated the mode in which the fructification was produced. Although the significance of this example could not be discovered when it was originally described, in the light of the fruiting specimens of *Neuropteris heterophylla* that have recently come into my hands (and which were collected from the "10 feet Ironstone Measures," which form the roof of the Thick Coal at Clays Croft Openwork, Coseley, near Dudley, and communicated to me for examination by Mr. H. W. HUGHES, F.G.S., Dudley), I think that there cannot remain any doubt that the Blairpoint specimen of *Neuropteris heterophylla* exhibits the pollen-bearing organs of the species.

Fig. 1. — *Neuropteris heterophylla*, BRONGT., showing "male inflorescence." Nat. size. (In collection of Geol. Survey of Scotland, Edin.)

Among the specimens which were submitted to me for examination from Coseley, which are preserved in small ironstone nodules, were three examples of a *Rhabdocarpus*, each attached to a fragment of a pedicel bearing the foliage of *Neuropteris heterophylla*, BRONGT.

The specimens are shown on Plate 1, figs. 1–9.

* See SCOTT, 'Studies in Fossil Botany,' p. 374, *et seq.*, 1900.

† "On the Fructification of some Ferns from the Carboniferous Formation," 'Trans. Roy. Soc. Edin.,' vol. 33, p. 150, Plate 8, fig. 7.

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Figs. 1 and 9 are the two halves of the same nodule, shown natural size. Fig. 2 is the specimen shown at fig. 1, enlarged two times. Of the specimen shown natural size at fig. 3, there was only one-half preserved, and this is given magnified two times at fig. 4. Figs. 5 and 7 show the two halves of the same nodule, natural size, and these are shown magnified two times at figs. 6 and 8.

The seeds are all about 3 centims. long; probably the specimen shown at figs. 1 and 9, if it had been perfect in the upper part, would have been slightly longer; their width varies from about 1·10–1·40 centims. Their general form is oblong, but they are gradually contracted from about the middle into a somewhat sharp point.

The outer surface shows numerous longitudinal ribs, formed by bands of sclerenchymatous tissue in the outer envelope of the seed.

On the specimen shown at figs. 1, 2, and 9, the apex is truncate, but this is the result of imperfect preservation, the apex having been broken off. The true form of the seed is seen at figs. 3–8, where the apex forms a micropylar point. The example seen at figs. 1, 2, and 9 is uncompressed, and shows that the seeds were circular in transverse section.

These seeds, if separated from the foliage, would find a place in the genus *Rhabdocarpus*,* and differ little from *Rhabdocarpus tunicatus*, as figured by Renault,† or *Rhabdocarpus subtunicatus*, as figured by Grand'Eury,‡ except in being narrower in proportion to the length.

The internal organisation of *Rhabdocarpus* has been described by Brongniart§ and Renault.‖ It belongs to the *Radiospermeæ* group of the "older Gymnosperms,"¶ but differs much both in size and type of structure from that met with in *Lagenostoma Lomaxi*, the seed of *Lyginopteris Oldhamia*.**

The examples given at figs. 2 and 4 (specimens, figs. 1 and 3 (× 2)) show fragments of the pedicel—in these cases probably the termination of pinnæ—but the rachis is much thicker than it would be in ordinary barren pinnæ, a necessity for the support of so large a seed. Two pinnules are seen attached to the rachis at *a*, fig. 2, and one

* Göppert and Berger in Berger, "Fructibus et seminibus," p. 20, Vratislaviæ, 1848.

† Renault, 'Flore foss. Terr. houil. d. Commentry' (Part II.), p. 638, Plate 72, fig. 19, 1890.

‡ Grand'Eury, 'Geol. et Paléont. du bassin houil. du Gard,' p. 328, Plate 6, fig. 6, 1890.

§ Brongniart, 'Recher. sur les graines fossiles silicifiées,' pp. 21, 23, Plates 9–12, 1881. *Note.*—Brongniart ascribes to *Rhabdocarpus* characters not included in the original description of the genus. Brongniart's *Pachytesta*, as judged by external characters, would also find a place in *Rhabdocarpus* G. and B., thus, according to the Brongniartian view, the seed of *Neuropteris* should perhaps be placed in *Pachytesta*.

‖ Renault, 'Cours d. Botan. Foss.,' vol. 1, p. 110, 1881; also 'Bassin houiller et permien d'Autun et d'Épinac,' fasc. IV.; 'Flore Foss.,' Deux. partie, pp. 387–9, 1896.

¶ See Oliver, "The Ovules of the Older Gymnosperms," 'Ann. of Botany,' vol. 17, No. LXVII., p. 451, 1903.

** Oliver and Scott, "On *Lagenostoma Lomaxi*, the Seed of Lyginodendron," 'Roy. Soc. Proc.,' vol. 71, p. 477, 1903.

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at *a* on fig. 4. These do not differ in form or nervation from the ordinary foliage pinnules of *Neuropteris heterophylla*. Figs. 6 and 8, enlargements of figs. 5 and 7, also show a fragment of rachis. The pinnule shown at *a*, fig. 8 (× 2) is not seen on the other half of the nodule given at fig. 6 (× 2). This pinnule, fig. 8 (*a*) is also typical of the foliage of *Neuropteris heterophylla*. That shown at (*a*), fig. 6, shows a slight widening of the base, and seems to be attached to a basal expansion somewhat of the nature of a cupule. This semi-cupule-like structure is better seen at (*b*), especially on fig. 8 (× 2). It does not seem to form a complete cupule surrounding the seed as in *Lagenostoma Lomaxi*, but is more in the form of a subtending tract, and probably served as a protection to the seed during the early stages of its development.

The main rachis of *Neuropteris heterophylla* bore many large Cyclopteroid pinnules,* whose function, the protection of the young growing points, was similar to that performed by *Aphlebia* on *Dactylotheca plumosa*, ARTIS sp.,† and other genera.

The interest in the Coseley specimens is threefold. They enable us now, I believe, to explain the specimen of *Neuropteris heterophylla* from Blairpoint, to which reference has been already made. Of this example there cannot be any doubt as to its also belonging to *Neuropteris heterophylla*, BRONGT., as the foliage attached on the lower portions of the pinnæ agrees absolutely with the pinnules of that species, and though one cannot decipher the minute structure of the bodies which terminate the naked slender dichotomous branchlets, the occurrence of two forms of fructifying organs on the same species seems to preclude the possibility of doubting that in the Blairpoint specimen we see the remains of the organs which produced the necessary pollen grains for the fructification of the Rhabdocarpous seed, and it is further seen that at least some of the numerous seeds referred to the genus *Rhabdocarpus* belong to the Cycadofilices.

The Blairpoint and Coseley specimens also afford the first case where the male and female organs of a single species are known which belongs to that large and important group of carboniferous plants now included in that somewhat undefined assemblage which we call the Cycadofilices.

* ROEHL, 'Fossile Flora d. Steinkohlen-Formation Westphalens,' p. 37, Plate 17 (*Neuropteris Loshii*, BRONGT. = *Neuropteris heterophylla*, BRONGT.).

† L. and H., 'Fossil Flora,' vol. 2, Plates 100 and 101 (*Sphenopteris crenata* and *Schizopteris adnascens* = *Dactylotheca plumosa* ARTIS, sp.). KIDSTON, 'Trans. Roy. Soc., Edin.,' vol. 38, p. 216, Plate 2, figs. 6–7 (1896).

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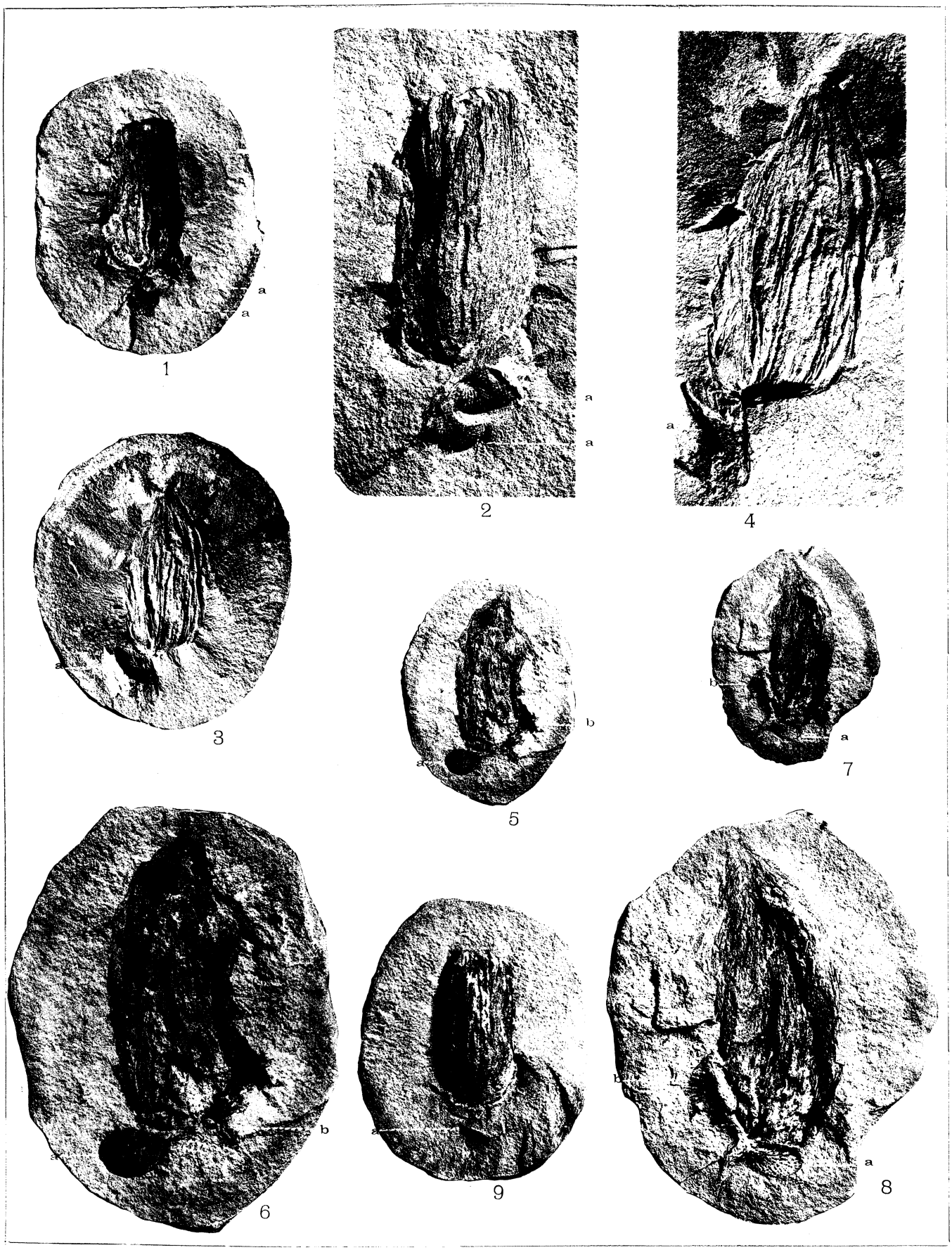

R. Kidston, Photo. *Morgan & Kidd, Collo.*

Neuropteris heterophylla, Brongt.

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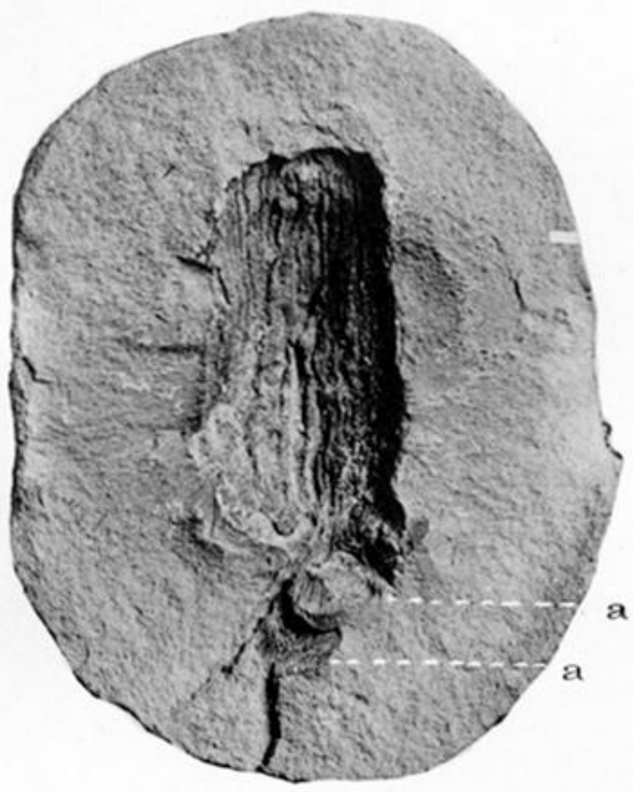

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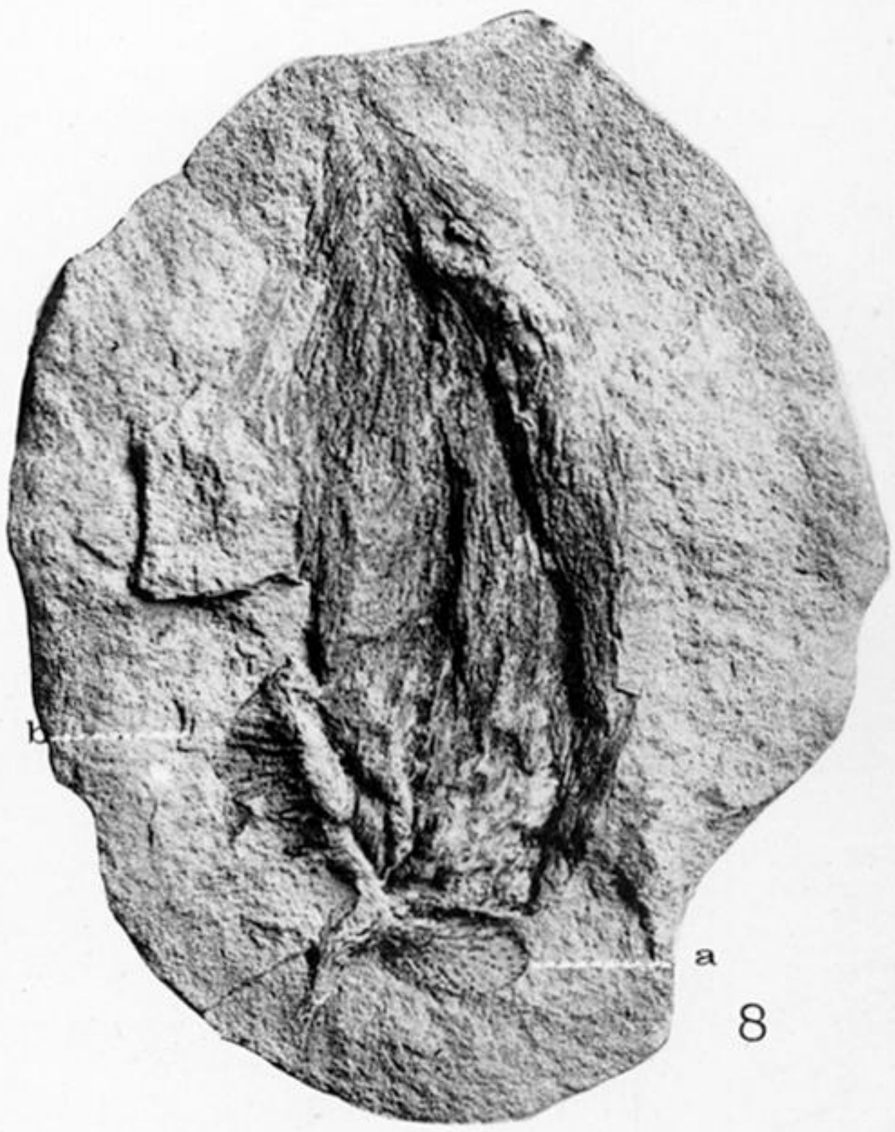

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Neuropteris heterophylla, Brongt.